Plate 8.—*Solanum atropurpureum.*

Under experiment for 28 days.

A. Plants grown in ordinary air.

B. ,, in air containing 11·4 parts of CO_2 per 10,000.

Plate 9.—*Fuchsia.* Dark-leaved variety.

Under experiment for 28 days.

A. Plants grown in ordinary air.

B. ,, in air containing 11·4 parts of CO_2 per 10,000.

Plate 10.—*Fuchsia.* Dark-leaved variety.

Under experiment for 54 days.

A. A plant grown in ordinary air.

B. ,, in air containing 11·4 parts of CO_2 per 10,000.

N.B.—The scale on the rod is in inches.

"On the Influence of an Excess of Carbon Dioxide in the Air on the Form and Internal Structure of Plants." By J. Bretland Farmer, D.Sc., F.R.S., Professor of Botany in the Royal College of Science, London, and S. E. Chandler, A.R.C.S.

Received May 6,—Read May 29, 1902.

The plants which form the subject of the present enquiry were kindly handed over to us by Messrs. Horace Brown and F. Escombe. They were preserved in alcohol, and had previously served as the material on which the researches of these investigators on the influence of varying amounts of carbon dioxide in the air on the photosynthetic processes of leaves and on the mode of growth of plants* had been conducted.

The series, consisting of the following five plants, viz., *Kalanchoë Welwitschii*, *Solanum atropurpureum*, *Begonia gracilis*, *Impatiens platypetala*, *Fuchsia*, sp., included in every case specimens which had been grown in a greenhouse in ordinary air containing 3·29 parts of carbon dioxide in 10,000 volumes of air, and others that had been cultivated under conditions as similar as possible except that the atmosphere contained about 3·5 times (11·47 per 10,000) the amount of carbon dioxide normally present in ordinary air. For the sake of brevity we shall refer to them as the *air* or control and as the *CO_2* plants respectively.

We directed our attention more especially to the following points :—

(1.) The relative dimensions of the internodes.

* *Cf.* H. Brown and F. Escombe, "On the Influence of Varying Amounts of Carbon Dioxide in the Air on the Photosynthetic Processes of Leaves and on the Mode of Growth of Plants," 'Roy. Soc. Proc.,' vol. 70, in which full details are given as to the methods of experiment and the external appearances presented by the plants.

(2.) The average relative areas of the leaves.

In order to obtain this estimate the leaves were traced on paper, the pattern then cut out, and the average weights of each series obtained.

(3.) The number of stomata per unit of area of leaf surface, and also the *relative number of stomata and epidermal cells* per unit area. The object of the latter determination is to endeavour to ascertain whether any observed alteration in the total number of stomata per unit of area should be ascribed to an alteration in the degree of development reached by the epidermal cells, or whether it is to be referred to a direct increase or decrease of the stomata as the result of the influence of the added carbon dioxide.

(4.) The anatomical differences in the stems and leaves.

(5.) The relative amount of starch and other cell-contents in the two series.

The drawings which illustrate this communication are all drawn carefully to one scale, and are therefore strictly comparable for purposes of measurement.

Kalanchoë Welwitschii.—The average length of the four youngest internodes in the air plant as compared with those of the CO_2 plant is in the proportion of 1·0 : 0·75, taking those of the air plant as unity. If the development of the internodes in the two series be traced backwards, it is found that the CO_2 plant attains to its final internodal length sooner than does the air plant. Thus in one example, whilst the full length was reached in the CO_2 plant at the third or fourth internode, it was not till the fifth that further extension ceases in the air plant. The effect of this is to further emphasise the stunted appearance characteristic of the CO_2 series.

The leaves differ greatly in the two sets, being larger (1·0 : 0·17), thicker (1·0 : 0·7), and more broadly ovate and serrate in the air-grown specimens. As regards the stomata, the guard cells were of approximately equal size in both series, but were always widely opened in the CO_2 plants, whilst they were closed in the control. This points to a permanent alteration of form, seeing that the material throughout was already killed and preserved in spirit. A similar difference in the appearance of the guard cells we found to be very constantly exhibited by all the other species examined by us.

The numerical proportion of the stomata in the two series per unit of leaf (under) surface was about 1·0 : 1·5 (fig. 1, A and B); but this is largely due to the decreased size of the rest of the epidermal cells in the plant treated with carbon dioxide. This is proved by ascertaining the ratios between the number of epidermal cells and stomata in the two series respectively; it is found to be 100·0 : 7·3 for the air plant and 100·0 : 7·1 for the CO_2 specimen. It thus appears that in *Kalanchoë* there is no material disturbance of the normal

proportion existing between the epidermal cells and stomata as a consequence of the added carbon dioxide. It will, however, be clear that the small leaves of the latter series do possess, area for area, a far greater number of stomata than do the leaves of the control plants.

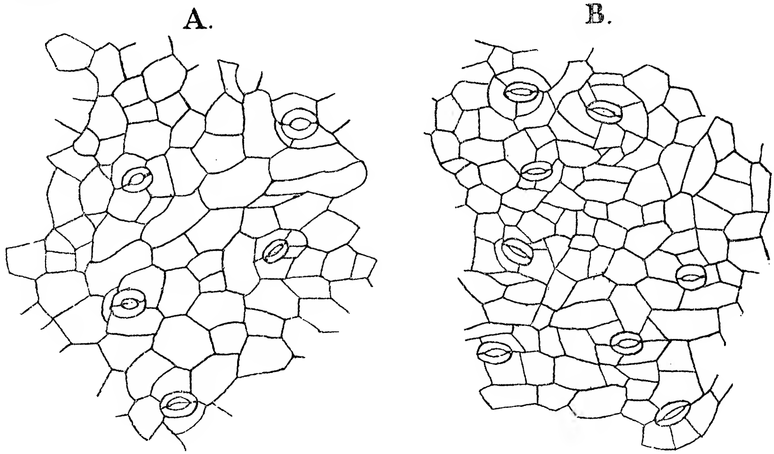

Fig. 1. *Kalanchoë Welwitschii,* epidermis of the underside of the leaf. A, air-; B, CO_2-plant.

In the anatomical or internal structure the differences are not so great as might perhaps have been anticipated. They chiefly affect the amount of xylem vessels and tracheids produced, and also the degree of differentiation of the mechanical tissues.

The vascular bundles are commonly less in number in the CO_2 than in the control plants, and the xylem of the former is always more parenchymatous in character than is that of the latter series in which the tracheids and vessels are tolerably uniformly distributed (see fig. 2). The phloem is, however, equally well developed in the bundles of both series. The stem of the air-grown plants is provided with a well-marked hypodermal collenchyma and pericyclic sclerenchyma, and in both respects it surpasses the CO_2 plant in the degreee of development marked by these tissues. We consider that the reduction in the conducting elements of the xylem is probably to be chiefly correlated with the diminished leaf surface, and the consequent lower transpiration, for the total number of stomata on the small leaves is far short of that present on the normal plants. The comparative poverty in mechanical tissue is perhaps partly connected with nutritional disturbances, and partly with the diminished weight of the growing organs of the plant. For it is known that the degree of differentiation of mechanical tissues is subject to modifications depending on the amount of stress or strain imposed upon the growing organs.

As regards the structure of the leaf, the character of the mesophyll does not differ, except in amount, in the two cases.

The roots showed no difference whatever in structure in the two series.

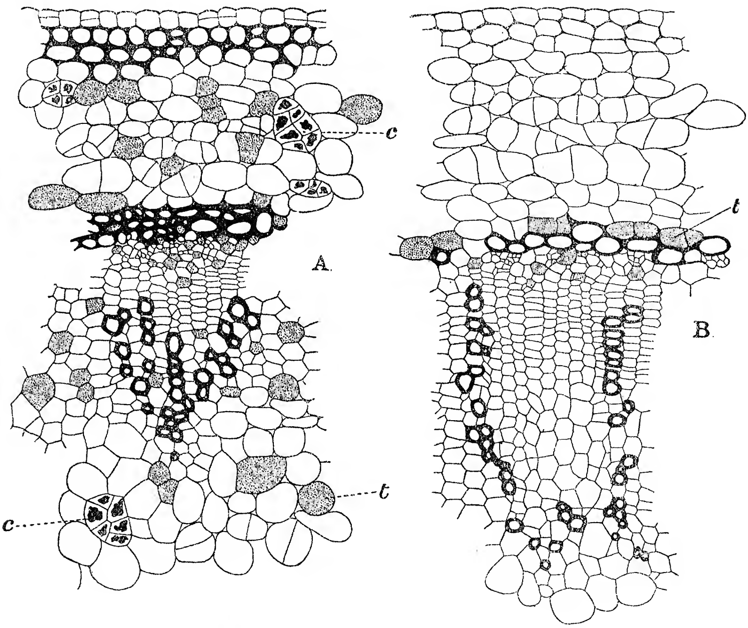

FIG. 2. *Kalanchoë Welwitschii*, transverse section of the stem. A, air- ; B, CO_2-plant.

Kalanchoë stands alone amongst the plants we examined in one respect. The specimens which had been exposed to the additional carbon dioxide exhibited no increase in the amount of starch present in their leaves or cauline parenchyma. But a difference was indicated between the metabolic proceeds of the CO_2 and air plants respectively in two other particulars. Firstly, the air plants contained large quantities of tannin-cells, especially in the vicinity of the vascular bundles. These were very much fewer and far less striking in the CO_2 plant. Again, the air plants possessed crystal-containing cells of remarkable form in the pith. These occur in groups, each group having arisen by the division of a single mother cell, the limits of which can still be traced. Each cell thus produced contains crystals of calcium oxalate. These special cell groups were entirely absent from the CO_2 plants; and when crystals occur in them, as they do very occasionally, they are found in ordinary unspecialised cells of the ground tissue.

Solanum atropurpureum.—The general tendency towards a stunted

appearance on the part of the CO_2 plant is also manifested by this species.

Comparing the total average length of the five youngest internodes in each specimen, the proportion was found to be 1·00 : 0·65, but nearer the base of the specimens this relation was reversed. The amount of material at our disposal did not, however, enable us to determine whether this is to be regarded as an accidental variation, though we incline to think it is not so. Possibly it may be connected with the fact, which obtains here, as in *Kalanchoë*, that the full size of internode is reached sooner in the control than in the CO_2 plants.

The stem and leaves are armed with spines which were somewhat more numerous and very much better developed in the normal (control) plants.

The proportion existing between the size of the leaves in the air and CO_2 plants respectively is 1·0 : 0·6. As regards the anatomical differences these are in the direction such as might have been anticipated from a consideration of the diminished leaf surface. The xylem is less well developed in the experimental than in the control plants, whilst the phloem again shows but little variation. The hypodermal collenchyma is not so well marked in the CO_2 as in the air plant, exactly as is the case with *Kalanchoë*.

The mesophyll of the leaf was somewhat more spongy in the CO_2 plant than in the control, a fact perhaps to be correlated with the greater number of stomata in the former.

No difference was observed in the structure of the roots of the two series.

The number of stomata per unit area of leaf surface was greater in the CO_2 than in the air plant in the proportion of 1·0 : 1·3. The relative number of epidermal cells and stomata in the two series was 100 : 43 (air) and 100 : 48 (CO_2) respectively.

The cells of the leaves (including the guard cells) and of the wood parenchyma were gorged with starch in the case of the CO_2 plant, and the guard cells of the stomata were widely open as contrasted with their closed position in the control specimen.

Begonia gracilis.—The relation between the average lengths of the four youngest internodes in the two series is expressed by the ratio 1·0 : 0·5 for the air and CO_2 plant respectively. But the internodes of the latter do not reach their full length as soon as do those of the control plant: in this they resemble the foregoing species.

The proportionate size of the leaves in the two series is about 1·0 : 0·56.

The stomata in the leaves of this plant are aggregated in groups, these being separated from one another by large epidermal cells, that junction as water-storage elements. The leaves of the CO_2 plant contain a larger number of stomata per unit area than those of the control plant, the

proportion being 1·0 : 2·3 (fig. 3, A and B). But this large increase of the number in the case of the experimental plant is solely due to a diminished size of the water-storing epidermal cells, whereby a larger number of stomatal groups are included in a given area. There is no average increase of the number of the stomata within a group, and hence the disparity is clearly due to the effect of the additional carbon dioxide in arresting the growth of the ordinary epidermal cells before they have reached their full size. The guard cells are similar in size in the two series, and are not affected in the same way as the rest of the epidermis.

The anatomical structure of the stem and leaf presents no features of special interest beyond the character of the epidermis just described. The remaining differences were of a minor character, and of too little constancy to warrant any general points of distinction being traced between the two sets of plants.

No difference was observed between the root structure in the two series.

The cells of the leaf and of the ground tissue of the stem were densely filled with starch in the case of the CO_2 plant, but not strikingly so in the control specimen. Furthermore, the latter was rich in crystals of calcium oxalate, which were absent from the CO_2 plant. This is of some importance, as indicating that probably the lack of starch in the air plant is to be connected with the utilisation of the carbohydrate, which in the other is simply stored up in an insoluble form. A similar relation exists in the other species in which these crystals occur.

Impatiens platypetala.—The proportion between the sizes of the leaves in the air and CO_2 plants was found to be 1·0 : 0·76. Owing to the difficulty encountered in securing suitable preparations of the epidermis, no estimates were arrived at as to the comparative numbers of stomata.

As regards the internal anatomy, the relation between the relative development of the conducting elements of the xylem showed, as was to be expected, the same kind of difference as in the case of the plants already described. In the leaf, the CO_2 specimen had the advantage in thickness and in the size of the cells. The contrast was most striking in the palisade layers, which were distinctly double in the experimental plant, as compared with the slight elongation characterising the cells of the corresponding layer in the control plant (fig. 4, A and B). The intercellular spaces were also larger and more numerous in the former.

The cells of the CO_2 plant contained very large quantities of starch, as in the examples previously described, and crystals of calcium oxalate also occurred, though not so abundantly as in the tissues of the control plant.

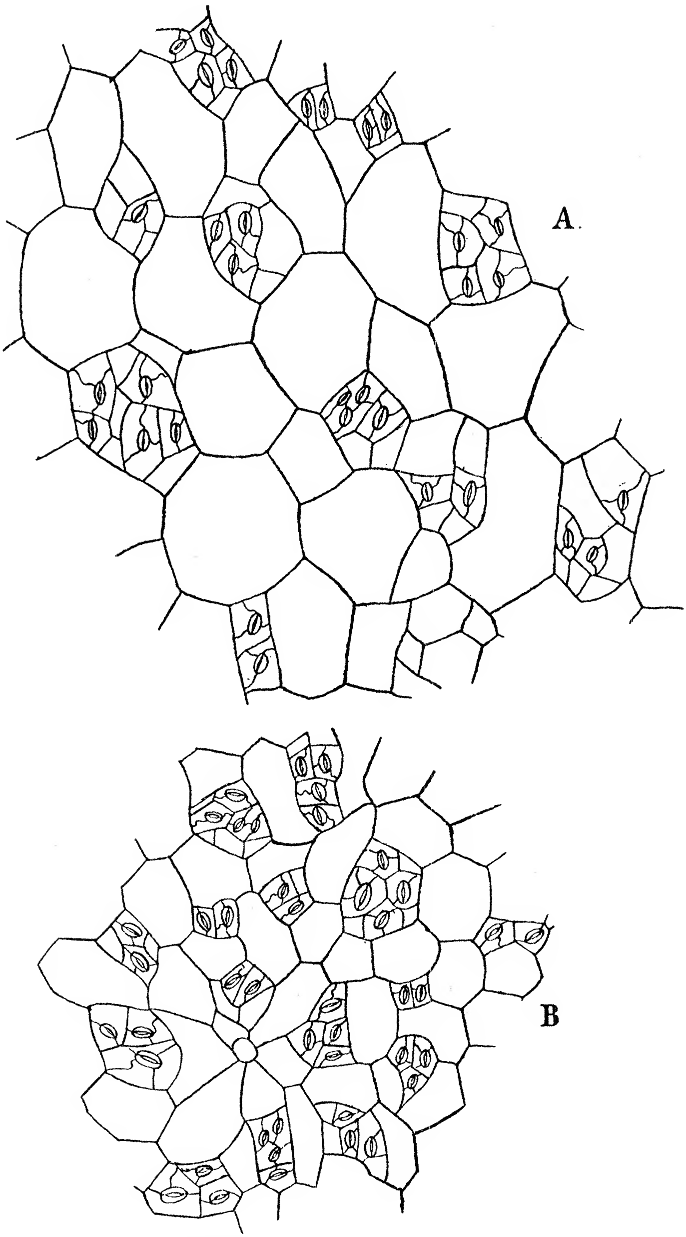

FIG. 3. *Begonia gracilis*, epidermis from lower surface of leaf. A, air- ; B, CO_2-plant.

Fuchsia, sp.—The remarkable appearances presented by the experimental plants have been described by Brown and Escombe in their

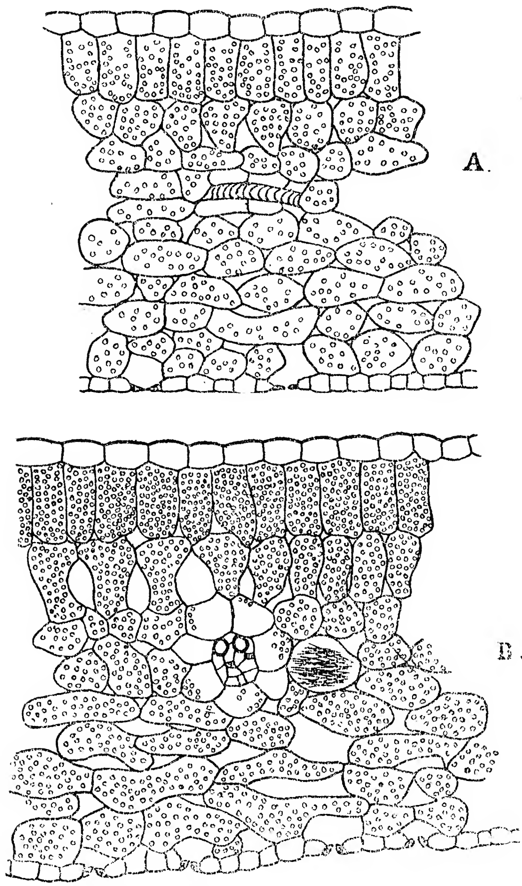

Fig. 4. *Impatiens platyphylla*, transverse section of leaf. A, air-; B, CO_2-plant.

paper already referred to. No very satisfactory measurements were made of these internodes with a view of ascertaining their relative lengths, but in a general way the appearance presented by the two series conformed to that already described for the other species.

The proportionate size of the leaves in the two series was estimated as 1·0 : 0·35.

The numerical relation of the stomata per unit area of leaf in the two cases is 1·0 : 1·4 (fig. 5, A and B), but the proportion of epidermal cells to stomata in the two series respectively proved to be almost identical, being 100 : 32 (air) and 100 : 31 (CO_2).

The only feature of anatomical difference in the stems of the two series consisted in the inferior differentiation of secondary wood in the CO_2 plant, whilst the phloem was equally well developed in both.

The roots were perfectly similar in the two series. Starch occurred in much larger quantity in the leaf, and ground parenchyma of the CO_2 plant than in the control example. Crystals of calcium oxalate occur in the leaves of both series, and appeared to be about equally distributed over equal areas.

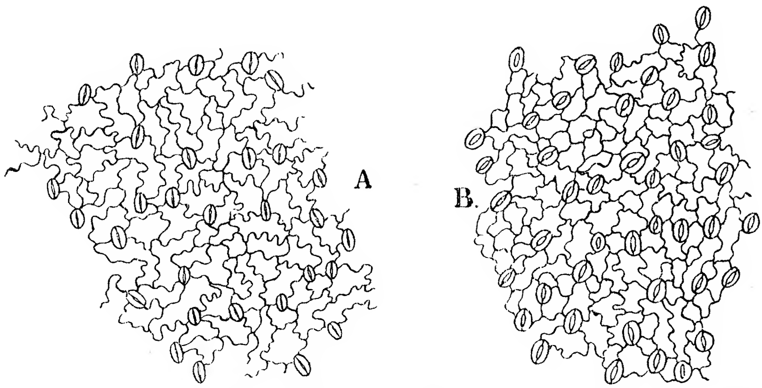

FIG. 5. *Fuchsia*, sp., epidermis from lower surface of leaf. A, air-; B, CO_2-plant.

The results upon the structure of flowering plants, consequent on increasing the amount of carbon dioxide normally present in the atmosphere to about three and a half times this amount (*i.e.*, when it is present in the proportion of about 1 in 1000 volumes) may be briefly summarised as follows:—

1. The growth of the internodes is checked, and the period of growth as measured by the elongation of successive internodes is lengthened.

2. The growth in surface of the leaves is arrested at a more or less early stage.

3. The absolute number of stomata *per unit area* of leaf surface is considerably increased, largely or entirely as the result of the non-attainment by the epidermal cells of their normal size. The guard cells of the stomata do not however share in this diminution, but are, if anything, larger in plants treated as above. The guard cells also are gorged with starch, and the stoma remains open even when the leaf is killed in spirit. The *relative* proportion of the stomata to the number of epidermal cells in a given area, remains approximately constant for both leaves treated with the additional carbon dioxide, and those which have been grown under normal conditions. But although the stomata show the increase in number just referred to, their total number on the whole surface of a treated leaf may be smaller, on

account of the great diminution in the size of the latter as compared with that of the plant grown under normal conditions, and because the total number of the whole epidermal cells in the smaller leaves may also be smaller than that of the epidermis of a normal leaf.

4. The anatomical structure of the internal tissue of the leaves is not materially altered, any modification that may arise consisting chiefly in the relative number of cell layers, and of the abundance of intercellular spaces formed.

5. The anatomical structure of the stem commonly differs in the direction of the formation of less lignified elements of the xylem, a smaller number of vessels, and frequently also in the imperfect development of the mechanical tissues. The phloem, on the other hand, shows no alteration. The change in the xylem is almost certainly related with the diminished leaf surface, and consequently reduced transpiration. But bearing in mind the stomatal relations mentioned under 3, it is probable that the reduction is also connected with disturbances of the metabolic processes which may act, not only in the way here indicated, but also may more directly affect the means of supplying material for the growth in thickness of the cell walls.

6. The last point is emphasised by the invariable accumulation (except in *Kalanchoë*, and it will be remembered that the metabolic processes of succulent plants are frequently peculiar) of starch in the leaves and ground parenchyma of the treated plants. As regards *Kalanchoë*, the guard cells of the stomata, which are in many respects comparatively isolated from the other tissues, do contain more starch in the treated than in the normal plants. It is also worth noting that in this plant the tannin so characteristic of the specimens grown under normal conditions is very much reduced in the experimental series, a fact which further points to a disturbance of the ordinary course of metabolism.

7. No alteration could be detected in the roots as a consequence of the increase in the carbon dioxide contents of the atmosphere.

8. When crystals of calcium oxalate occurred in a species they were always less abundant in the treated than in the control plants, with the possible exception of *Fuchsia*.

It remains to be stated that the results here described apparently differ in a remarkable way from those obtained by Téodoresco,* who investigated the action of increased carbon dioxide upon growth. The conditions of the experiment, however, in the two cases were by no means similar. Téodoresco compared plants which had been grown in an atmosphere entirely purified from carbon dioxide with others grown in air containing an amount varying from 1·5 per cent. to 2 per cent. of this gas. He found that under these conditions, the plants

* E. C. Téodoresco, "Influence de l'Acide Carbonique sur la Forme et la Structure des Plantes," 'Rev. Gén. de Botanique,' vol. 11, 1899.

treated with the excessive carbon dioxide grew more luxuriantly, and exhibited more complete internal differentiation than those deprived of this source of carbon.

This result is perhaps hardly surprising, as the one set of his plants was entirely deprived of its source of atmospheric carbon dioxide, and it would have been interesting to have compared his specimens at the end of the experiment with others grown in normal air, but otherwise under similar conditions of temperature, illumination, &c.

It is, however, worthy of notice that Téodoresco kept the atmosphere round his plants in a tolerably dry condition by means of sulphuric acid. This might tend to promote transpiration, and it may be that the apparent discrepancies between his plants and our material as regards both structure and histological differentiation is partly perhaps to be attributed to this circumstance. But only further investigations can settle this and many other points of interest connected with the influence, direct as well as indirect, of alteration in the constitution of the atmosphere on plant-structure.

"Preliminary Report on the Recent Eruption of the Soufrière in St. Vincent, and of a Visit to Mont Pelée, in Martinique." By Tempest Anderson, M.D., B.Sc., F.G.S., and John S. Flett, M.A., D.Sc., F.G.S. Communicated by the Secretaries of the Royal Society. Received August 11, 1902.

[Plates 11–13.]

Dr. Tempest Anderson and Dr. John S. Flett, who received a commission from the Royal Society to investigate the recent volcanic eruptions in the West Indies, more especially in St. Vincent, submit the following preliminary report:—

We arrived at Barbados on June 8 (having left London on May 28), and thence proceeded to St. Vincent, where nearly 4 weeks were spent, mostly at Chateaubelair and Georgetown, in the vicinity of the Soufrière. On June 29, Dr. Tempest Anderson went to Grenada to examine the lagoon at St. George's, returning some days later, Dr. Flett remaining at St. Vincent to complete his investigations.

On July 6 we arrived at Martinique, and on the 12th left that island for Dominica, where we remained until July 17, when we returned to Barbados. In all 6 weeks were spent in the West Indies.

In the Windward Islands, in the month of July—the middle of the rainy season—the work of a geological expedition is necessarily attended with many difficulties, but these were greatly mitigated by the kindness rendered by all with whom we came in contact. To Sir Robert Llewellyn, K.C.M.G., the Governor of the Windward Islands, and to the Administrators of St. Vincent, St. Lucia, and

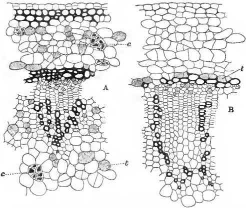

FIG. 2. *Kalanchoe Welwitschii*, transverse section of the stem. A, air-; B, CO_2-plant.